Community phylogenetics of forest trees along an elevational gradient in the eastern Himalayan region of northeast India

Stephanie Shooner

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By: **Stephanie Shooner**

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Signed by the final Examining Committee:

_____ Chair

Dr. J. Grant

_____ Examiner

Dr. G. Brown

_____ Examiner

Dr. J. Jaeger

_____ Examiner

Dr. J-.P. Lessard

_____ Supervisor

Dr. S. Dayanandan

_____ Supervisor

Dr. T.J. Davies

Approved by _____

Dr. S. Dayanandan, Graduate Program Director

Date: _____ _____

Dean of Faculty

Abstract

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Large-scale environmental gradients have been invaluable for unravelling the processes shaping the evolution and maintenance of biodiversity. Gradients provide a natural setting to test theories about species diversity and distributions within a landscape with changing biotic and abiotic interactions. Elevational gradients are particularly useful because they often have an extensive climatic range within a constricted geographic region. Arunachal Pradesh is the northeastern-most province in India, located on the southern face of the eastern Himalayas. This region is considered a biodiversity "hotspot", with an estimated 6000 flowering plant species of which 30-40% are endemic. For this thesis, I analyzed tree communities in plots distributed throughout the province using both species and phylogenetic diversity indices. I explored shifts in community structure across elevation and space as well as the biotic and abiotic forces influencing species assembly throughout the landscape. Species richness and phylogenetic diversity decreased with increasing elevation, as theory predicts. However, species relatedness did not show a clear pattern with elevation. Nonetheless, by exploring beta-diversity (both taxonomic and phylogenetic), I was able to show a strong effect of environmental filtering with elevation. Environmental filtering is generally associated with species clustering on the phylogeny, where co-occurring species in a community are more closely related than expected by chance. Here, however, I suggest that forest community structure is driven by filtering on glacial relicts, resulting in random or over-dispersed community assemblages. These patterns point to possible regions for conservation priority that may provide refugia for species threatened by current warming trends.

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PART I: Introduction

One of the most important questions in ecology is why some species occur where they do and not elsewhere. The answer to this question is not a simple one; it encompasses a seemingly endless list of factors and their putative interactions. Important within this list are climate, elevation, species × species interactions, energy availability, and the adaptiveness of a given species. There are various analytical approaches that consider these factors either separately or in some combination, and often within an ecological gradient. In this thesis I explore one approach in particular, the relatively new field of phylogenetic community ecology (community phylogenetics). First described in detail by Webb et al. in 2002, community phylogenetics aims to capture the interaction among species assemblages, phylogeny and traits. In the following work I focus on the interface between species assembly and phylogeny, drawing inference from the phylogenetic structure of the species present in a community assemblage.

Brief history of community phylogenetics

The field of community phylogenetics built on previous ideas of species co-occurrence (Cody and Diamond 1975, Connor and Simberloff 1979, Gotelli and Graves 1996, Gotelli 2000), and merged this with advances in phylogenetic theory. Among the first to hypothesize about the nature of biotic interactions (species × species interactions), Darwin (1859) suggested that species from the same genus would experience stronger competition than more distantly related species from different genera on the basis that those species from the same genus were more ecologically similar due to their shared evolutionary history. Many years later, Elton (1946) empirically tested Darwin's hypotheses by examining species-genus ratios in various communities and found that the different genera present in the communities were rarely represented by more than one species. He thus inferred that competition may allow different genera of the same trophic level to coexist, but limited coexistence of species of the same genus. Elton was also careful to suggest that it was necessary to distinguish between the ability of an individual to exist in a given environment and the ability to persist within a particular species assemblage. These ideas captured the essence of environmental filtering and limiting similarity

among related species as well as early ideas of niche filling within a community. Environmental filtering is the process by which abiotic factors structure species assemblages. At large scales, environmental filtering is thought to be a major determinant of species range, while at small scales it can contribute to niche heterogeneity (e.g. through variable soil or moisture). Conversely, limiting similarity describes the biotic interactions that can structure species coexistence. If species are sufficiently similar in their resource-use (niche) or phenotypic features, it is often presumed that they cannot coexist. Environmental filtering and biotic interactions can be inferred from patterns of phylogenetic relatedness, discussed below.

The implementation of pairwise co-occurrence matrices improved understanding of the theory of limiting similarity by allowing researchers to identify pairs of species that rarely or never occurred together, providing an important step towards identifying the processes responsible for the competitive exclusion of species within the environment (Cody and Diamond 1975). However, early results proved controversial as patterns were not compared to any null expectation, and thus remained largely descriptive. With the development and popularization of null models, these patterns in species assembly could be rigorously tested against a null hypothesis of random species associations (Gotelli and Graves 1996). These crucial milestones within ecology provided the foundation from which present-day community ecology and phylogenetic theory emerged.

Improving phylogenies

Another important factor in the development of modern community phylogenetics was the improvement of sequencing technology that allowed for better phylogenetic reconstructions. Traditionally estimated from shared phenotypic traits, phylogenies are now quantifiable using sequence information and fossil calibrations to inform divergence times among clades. With the advent of PCR in the 1980s, and more recently, next generation sequencing technology, molecular data can be generated quickly and cheaply, making the phylogenetic reconstruction of many 100's or even 1,000's of species possible (e.g. Plants: Davies et al. 2004, Mammals: Bininda-Edmonds et al. 2007; Birds: Jetz et al. 2012; Zanne et al. 2014; Animals, plants and microbes: Hinchliff et al. 2015). These phylogenetic trees provide the raw material upon which the indices describing community structure are based. The improvement of sequencing technology also came with a growth in bioinformatics and computing power, allowing for the

development of analytical programs that could easily integrate evolutionary information (via phylogeny), community information and sophisticated statistical tests.

Patterns in community phylogenetics

In a seminal paper, Webb et al. (2002) reviewed and discussed the potential for phylogenetics in studies of community assembly and introduced the field of modern community phylogenetics. The authors suggested that the distribution of pairwise distances measured on a phylogenetic tree between species within a community could help elucidate the processes structuring community assembly. It was hypothesized that communities structured by the abiotic environment would include species that are more closely related than expected by chance, presenting as "clustered" on the phylogeny. Under this scenario, a clustered community structure suggests that the species present in a community share the same traits related to persisting in a particular environment, assuming such traits are evolutionarily conserved. By contrast, a community structured by competition would have species that are more distantly related than expected by chance, referred to as "over-dispersed" on the phylogeny, again assuming trait evolutionary conservatism. Over-dispersion is thought to be driven by competition for resources acting on conserved traits (i.e. the traits that describe the fit of a species to its abiotic niche are conserved on the phylogeny), where closely related species can undergo competitive exclusion stemming from the exploitation of similar resources (Wiens and Graham 2005, Losos 2008). However, Webb et al. (2002) acknowledge that an over-dispersed pattern could also suggest abiotic filtering, selecting for converged traits across many clades, and other more recent studies have suggested similar patterns of over-dispersion of clustering could arise from multiple processes (see *'Caveats and assumptions',* below).

Dimensions of diversity and phylogenetic metrics

There are several metrics for quantifying phylogenetic diversity patterns across a landscape, with new methods being continuously developed in the field. Below, I describe some commonly used metrics that I explored in the thesis.

Alpha diversity

RH Whittaker (1960) was the first to explicitly describe the three spatial dimensions of species diversity in a landscape: alpha, beta and gamma diversity. He proposed that the total species

diversity of a region is equal to the sum of diversity per habitat in the region and the differences in diversity among those habitats. In this thesis, I examine a relatively large region but assume a single species pool, defined as the sum of all the species recorded in the study plots; I thus focus on alpha and beta diversity, using both species and evolutionary information.

Phylogenetic diversity

Phylogenetic diversity (PD) was first described in the context of conservation prioritization, particularly for areas where knowledge of the species pool was limited. Faith (1992) outlined the challenges in determining priority from taxonomic diversity, namely that information on the diversity of characters represented within a community was often lacking due to our limited ecological knowledge on species in any given area or within any given clade—a problem that remains today. Calculating evolutionary distances among species could instead, it was argued, predict character diversity without quantitative measurements of those features (Faith 1992). Phylogenetic diversity is presently and generally calculated using molecular phylogenies to capture the evolutionary distances separating species. Several metrics of phylogenetic diversity have been developed (e.g. see Schweiger et al. 2008, metrics reviewed in Winter et al. 2013); this thesis uses Faith's PD, defined as the sum of the total phylogenetic branch lengths, including the root, for the species in a given community.

Species richness and phylogenetic diversity have been shown to be tightly correlated; communities with high species richness will also have proportionately higher PD (Schweiger et al. 2008). Incorporating a null model with the calculation of PD can disentangle phylogenetic diversity from species richness—revealing whether a community contains more or less evolutionary history than expected given its richness, helping distinguish between biotic and abiotic processes structuring a community. Standardized metrics of PD can also control for differences in species richness across samples (Proches et al. 2006).

Net-relatedness index

Similar to PD, the net-relatedness index (NRI) measures the standardized effect size of the relatedness of species within a community by comparing observed relatedness to expected relatedness given community species richness. More specifically, the net-relatedness index is equal to -1 times the standardized effect size of the mean pairwise distance among species. The

NRI of a community can be positive (clustered) or negative (over-dispersed) and centers around zero (random relationship among species). Values greater than 1.96 and less than -1.96 represent those that are two standard deviations from a mean of zero and can be indicative of significance (alpha=0.05), although significance testing is often formally assessed using randomizations. As discussed briefly above, species communities that are phylogenetically clustered are generally interpreted as being structured by the environment, where the traits important for persistence are conserved among closely related species. Conversely, communities that are phylogenetically over-dispersed are usually interpreted as being structured by competitive exclusion, where closely related species exploit similar niche spaces and therefore cannot co-exist. This metric is useful for exploring species assemblages in diverse or under-studied areas because it does not require extensive collection of trait data and can provide some insight into the relative strength of the biotic and abiotic factors structuring communities.

Beta diversity

Beta diversity, or turnover, is the difference in species composition across space. It can be calculated in a variety of ways to determine boundaries in species composition or the rate of change through space. Differences among communities can be analogous to the degree of similarity between communities and the conversion between similarity and dissimilarity is simple (dissimilarity = 1- similarity). In this thesis I calculate taxonomic beta diversity using Sorenson's index (eq. 1):

$$Eq.1:\ Sorenson's = \frac{2C}{A+B}$$

where A is the number of species in habitat A, B is the number of species in habitat B and C is the number of shared species between both habitats. The phylogenetic equivalent of Sorenson's index is *phyloSor*, a measure of the shared branch lengths between habitats. The equation for *phyloSor* is the same as Eq. 1, except that A, B and C are quantified in terms of phylogenetic diversity (Faith 1992) rather than taxonomic richness. *PhyloSor* was first proposed to describe the phylogenetic shifts in community composition in a montane ecosystem—allowing exploration of whether phylogenetic turnover was strictly consistent with species turnover or whether differences among communities occurred somewhere along the evolutionary branches of the phylogeny (Bryant et al. 2008).

Recently, additional work has reframed beta diversity as the total variance in species communities in a region (Legendre and De Cáceres 2013). With this approach, the variance (or total beta diversity of a region) can be partitioned into local (plot) and species contributions to beta diversity. The local contributions to beta diversity (LCBD) metric measures the relative uniqueness of the plots in a study in terms of their composition; the species contributions to beta diversity (SCBD) metric identifies species with high variance, or high abundance at relatively few sites. This approach offers a plot-level, hierarchical measure of beta diversity that provides some advantages over pairwise approaches, such as the Sorenson index, when evaluating diversity patterns across a complex, non-linear landscape.

Caveats and assumptions

Despite the growing use of community phylogenetic metrics for disentangling biotic processes from abiotic processes, such as those reviewed above, several concerns have recently been raised about the underlying assumptions on which they are based. When interpreting patterns of phylogenetic dispersion, the major assumption is that traits important for community assembly (determining niche differences as well as fitness differences) are conserved on the phylogeny and that closely related species will compete more strongly due to their ecological similarity (Chesson 2000). However, convergent evolution can confound ecological interpretations of phylogenetic clustering and over-dispersion, because similar traits may have evolved independently in several clades. This shortcoming was illustrated in a diverse oak system, where trait differences and niche preferences were well understood and could better explain the over-dispersed structure of oak communities, which may have otherwise been interpreted as competition (Cavender-Bares et al. 2004). Thus without adequate knowledge of the study system and the various fitness traits associated with individuals within a clade, over-dispersion could be misinterpreted as competition, especially when processes such as convergent evolution and local adaptation are important (Kraft et al. 2015). The assumption that traits are conserved on the phylogeny is certainly not true for all traits, and lack of significant phylogenetic structuring in communities is sometimes attributed to the lack of trait conservatism within a particular group of taxa. In addition, evidence for trait conservatism may be misinterpreted from processes such as dispersal limitation, extinction and predation (Crisp and Cook 2012).

Although the focus of this thesis is not on competition, analyses that infer competition from patterns of community relatedness alone have been heavily criticized. In one highly cited example, Mayfield and Levine (2010) questioned whether competition should necessarily result in over-dispersion. Expanding on work by Chesson (2000), the authors suggest that differentiating between environmental filtering and competition can be difficult because coexistence is a product of both niche differences and competitive asymmetries. Niche differences may allow distantly related species to co-occur if niche differences vary with phylogenetic distance, whereas competitive similarities might favor co-occurrence of more closely related species if competitive traits are conserved and necessary for persistence (plant height, for example). In other words, competition can lead to the coexistence of distantly related species as well as closely related species, depending on the traits conferring competitive advantage. While the integration of co-existence theory and community phylogenetics is relatively new, Godoy et al. (2014) have shown that competitive differences increase with phylogenetic distance but that there is no relationship between stabilizing niche differences and phylogenetic distance. If this result generalizes, we would then predict that closely related species would co-occur more frequently in communities dominated by interspecific competition. However, the authors find in results from their experiment that co-occurring species are evenly dispersed on the phylogeny (Godoy et al. 2014). In part, this result might reflect scale effects (the small scale used in their study may not have had sufficient environmental heterogeneity for meaningful niche differences to be detected), but it also reaffirms the difficulty in inferring process from pattern, especially given the myriad of factors likely structuring communities.

Additional difficulties in interpreting phylogenetic patterns are evident from recent new models that incorporate speciation, colonization and extinction effects (Pigot and Etienne 2015). Under these models, patterns of over-dispersion can be accounted for by evolutionary processes at the landscape scale, and thus should not be interpreted as competition or other ecological processes structuring community coexistence. Furthermore, few models account for the effects of positive interspecific interactions, such as facilitation, on phylogenetic community structure. Positive biotic interactions have not been investigated thoroughly (but see Callaway 2002, Valiente-Banuet and Verdú 2007, Butterfield and Callaway 2013) and could lead to either random or over-dispersed patterns under environmentally challenging conditions.

Another area of critique for the field is based on the models underlying trait evolution. Current metrics often implicitly assume that phylogenetic distance scales linearly with time; in other words, a trait will become increasingly different with phylogenetic distance at a constant rate. However, such an evolutionary mode may be rare. In a recent paper, Letten and Cornwell (2015) proposed a correction for the calculation of phylogenetic dispersion of a community to better match assumptions of a Brownian motion (BM) model of evolution, which is most commonly assumed in the phylogenetic comparative literature. If the true model of evolution is BM, linear scaling would result in over-weighing of taxa with long evolutionary branches (Letten and Cornwell 2015). Transforming phylogenetic distances by taking their square root could correct, at least somewhat, for the discrepancy between evolutionary time and taxa dissimilarity—reducing the weight of long evolutionary branches. However, this transformation is contingent on a Brownian model of evolution, which is unlikely to be the true model for all traits.

Although the field of community phylogenetics has made great strides in developing and testing the influence of evolution on community response to biotic and abiotic influences, many challenges remain. Currently, our interpretation of phylogenetic patterns is limited by our understanding of how processes such as competition, environmental filtering and facilitation affect community structure in nature. Community phylogenetic models are also limited and do not currently account for the more complex evolutionary processes of speciation, extinction and colonization. Thus the analysis of phylogenetic patterns is not straightforward, and multiple factors must be considered before we can attempt to infer process from pattern.

Phylogenetic community ecology along the elevational gradient

Elevational gradients are some of the most distinct gradients in ecology. Trends in species richness and abundances with elevation have been investigated extensively and have suggested several general patterns, most commonly a monotonically decreasing or hump-shaped relationship with species richness (Rahbek 1995). While patterns in species richness and the causes of its variation with elevation have been the subject of several reviews (e.g. Lomolino 2001, McCain and Grytnes 2010), the disparity of patterns among taxonomic groups and different regions of the world leaves many questions unanswered. Hypotheses on the elevational gradient in species richness most often relate to changes in climate. However, other factors such

as the species-area relationship, the mid-domain effect, and habitat heterogeneity have also been proposed, although evidence that these processes are primary drivers of richness gradients remains lacking (McCain and Grytnes 2010). Patterns of phylogenetic diversity have not been explored as intensively, but reported patterns of phylogenetic diversity along elevational gradients appear similar to gradients in species richness, perhaps unsurprisingly given the generally high covariation between taxonomic and phylogenetic diversity (see above).

Based on the large scale processes structuring biodiversity, we would expect that phylogenetic diversity would decline with elevation, paralleling patterns of species richness. We might also predict that species would be more over-dispersed at low elevations due to higher habitat heterogeneity and warmer temperatures conducive to higher productivity and therefore greater competition, while high elevational communities might be more clustered because of environmental filtering. However, one of the first studies to explore phylogenetic dispersion of montane communities found that plant communities were relatively more over-dispersed at high elevations than at low elevations (Bryant et al. 2008). One explanation for this counterintuitive pattern is greater facilitation at higher elevations, which has been shown to be important in montane herbs (Callaway et al. 2002). Hummingbirds and ants, however, tend to be phylogenetically over-dispersed at low elevations and clustered at high elevations (Graham et al. 2009, Machac et al. 2011), fitting better to our initial expectations, and supporting a trend for greater structuring by competition at low elevations and more structuring by environmental filtering at high elevations. More recent studies have suggested that patterns of phylogenetic dispersion might vary with phylogenetic lineage and node age (Ndiribe et al. 2013). In this thesis, I revisit the question of how communities shift in phylogenetic structure with elevation, evaluating metrics of both alpha and beta diversity, using data on tree communities across one of the largest elevational gradients on earth.

Although recent, phylogenetic approaches have become widely used across multiple fields in ecology. Interesting applications for community phylogenetics include succession following disturbance (Verdú et al. 2009, Letcher 2010, Shooner et al. 2015), conservation prioritization (Faith 1992, Forest et al. 2007) , extinction risk and host-parasite interactions (Parker et al. 2015, Farrell et al. 2015). Software allowing the rapid generation of phylogenetic hypotheses has also become more available (e.g. *phylomatic*: Webb and Donoghue 2005,

phyloGenerator: Pearse and Purvis 2013), allowing users to generate large phylogenies with ease. Phylogenic methods additionally correct for species non-independence, allowing us to create better and more robust hypotheses testing. In this thesis, my aim is not only to investigate questions on phylogenetic diversity in montane regions, but also to illustrate the benefits of combining multiple complementary metrics to elucidate large-scale diversity patterns across a gradient.

Objectives and Predictions

In this thesis I investigate diversity patterns of forest assemblages in Arunachal Pradesh, India. The sampling plots used in this study were established on the southern face of the eastern Himalayas—providing an extreme elevational gradient to test changes in community structure. I use both taxonomic and phylogenetic metrics to infer the processes most important for forest species assembly at the plot level. More specifically, I investigate patterns of phylogenetic dispersion (PD and NRI) and beta-diversity (taxonomic beta-diversity, phylogenetic beta-diversity, LCBD, PLCBD) in communities across the landscape, while considering the effects of space (geographical distance) and environment (elevation).

The objectives of this thesis are:

1. To describe forest (tree) diversity patterns along the elevational landscape. Arunachal Pradesh is a floristically unique region and studies of its species richness and diversity, particularly at the community level, have been limited.
2. To explore the relative strength of environmental filtering with elevation using metrics of phylogenetic dispersion and beta-diversity.
3. To locate sites with distinct tree species compositions, which might represent areas of particular conservation interest.

I make the following predictions:

1. The province will have high species richness and high phylogenetic diversity, but that richness will be greater at low elevations than at high elevations. Due to the extreme elevations of the Himalayas, colder climates at higher elevations are likely to act as a filter for cold-adapted species.

2. Environmental filtering will be stronger at high elevations. If traits for tolerance are conserved on the phylogeny, species at high elevations will be more closely related than expected by chance.
3. Phylogenetically unique sites will be located at higher elevations, and might represent climate refugia.

PART II: Phylogenetic diversity patterns in Eastern Himalayan forests reveal strong evidence for environmental filtering of evolutionarily distinct lineages

Introduction

Species diversity patterns have been extensively studied along a number of large-scale environmental gradients and have advanced our understanding of the processes shaping species assemblages. It is well established that species richness generally decreases with distance from the equator and with increasing elevation (Stevens 1989, Stevens 1992, Rahbek 1995, Lomolino 2001), likely driven by factors including climate, energy and potential evapotranspiration (Currie 1991, Givnish 1999, Hawkins et al. 2003), although opposing patterns have been observed (Rahbek 1995). However, a shortcoming of these observations is that analyses of richness patterns assume that species are equivalent and independent of one another, but evolutionary history might be an important additional factor shaping diversity gradients (Davies et al. 2004, Mittelbach et al. 2007, Davies and Buckley 2012, Kerkhoff et al. 2014). The potential importance of evolutionary process on diversity patterns has long been recognized. For example, hypotheses regarding the unusually high diversity in the tropics have described equatorial regions as either museums or cradles of diversity, concepts based on speciation and long-term extinction survival, respectively. Specifically, cradles of diversity are considered to have favorable climate conditions and diverse niche space, allowing for rapid radiation of certain lineages while museums are areas with persistent lineages and may represent refugia, where species have avoided extinction (Stebbins 1974). More recently, there has been growing appreciation that evolutionary history might structure not only richness, but also the composition of species assemblages (Webb 2000, Cavender-Bares et al. 2004, Vamosi et al. 2009). For example, closely related species might share similar ecological preferences and tolerances, and thus tend to be found in similar environments; however, at local scales, it is possible that

competitive displacement might occur among species if resource requirements are too similar (Chesson 2000, Webb et al. 2002).

By combining information on evolutionary history with a large scale environmental gradient, we explore diversity patterns in India's northeastern-most province, Arunachal Pradesh, home to the southern face of the Himalayas—the largest elevational gradient in the world. We use phylogenetically explicit metrics to unravel the evolutionary processes shaping the local flora, allowing us to explore shifts in community diversity and evolutionary structure with elevation. Current theory suggests that communities in abiotically harsher environments (such as those found at high elevations) will tend to be composed of more closely related species than predicted by chance because phylogenetic niche conservatism and strong environmental filtering would select for a subset of lineages adapted to these more extreme environments (Webb et al. 2002, Bryant et al. 2008). However, empirical studies have sometimes shown opposite trends with phylogenetic clustering at low elevations, or in warmer climates, and over-dispersion at higher elevations, or in colder climates (Bryant et al. 2008, Gonzalez-Caro et al. 2014).

Phylogenetic beta diversity can offer an additional perspective to diversity patterns as it allows easy partitioning of spatial and environmental drivers while also considering turnover of evolutionary history, or branches on the phylogeny (Graham and Fine 2008). Investigating phylogenetic turnover may help reveal shifts in clade membership among communities experiencing different abiotic conditions across the landscape, and may be more informative than simple measures of phylogenetic dispersion *sensu* Webb et al. (2002). Recent developments in beta diversity metrics allow us to additionally distinguish among the relative contributions of individual communities to the total beta diversity in a region (Legendre and De Cáceres 2013) – highlighting sites with particularly distinct communities. Such approaches can be simply extended to additionally consider phylogenetic diversity. In Arunachal Pradesh, high endemicity and habitat heterogeneity might affect both the phylogenetic structure of communities as well as the rate of turnover between communities perhaps leading communities in distinct environments to have distinct compositions.

The apparent conflict between theory and empirical studies on the relationship between community structure and elevation highlight the need for a better understanding of the multiple processes determining community assembly. For example, it is well recognized that the

convergent evolution of relevant traits in stressful environments could lead to over-dispersed or random patterns of community structure (Webb et al. 2002, Bryant et al. 2008, Read et al. 2014). Relict taxa – taxa that have shifted their ranges to refugia in montane regions during periods of warming, for example – could also have large influence on phylogenetic community structure, but have been less well studied (Birks and Willis 2008, Stewart et al. 2010). Previous work has explored the genetic imprint of refugia on intraspecific genetic variation and local population dynamics, often using methods from phylogeography (Hooghiemstra and van der Hammen 1998, Tribsch and Schonswetter 2003, Mayle 2004, Vargas 2007, Provan and Bennett 2008); but to our knowledge, the presence of such refugia has not been considered within the context of community phylogenetic structure. Relictual taxa that have survived successive climate-driven extinction cycles might often be range restricted (Habel and Assmann 2009) and phylogenetically distinct from the regional community (Fryxell 1962, Provan and Bennett 2008). The presence of relict species might thus tend to increase local phylogenetic diversity and shape patterns of community phylogenetic dispersion.

The Eastern Himalayan region offers a heterogeneous landscape along one of the largest elevational and climatic gradients on Earth, with vegetation varying from tropical forest to subtropical, temperate and gymnosperm-prominent alpine forest (Roy and Behera 2005). Unique to the Himalayas, the rapid transition between forest and climatic zones makes this region especially interesting for phylogenetic diversity studies despite remaining largely underexplored. Previous work in the Eastern Himalayas has suggested that the highest species richness occurs in forest transition zones, between tropical semi-evergreen to sub-tropical evergreen, and sub-tropical evergreen to broadleaf forests (Behera and Kushwaha 2007), and it is estimated that 30% - 40% of the ~6000 plant species in Arunachal Pradesh are endemic (Myers 1988, Baishya 1999, Roy and Behera 2005). While there are conflicting reports on the relative frequency and distribution of endemics in the region, with evidence for high endemism in both the low-elevation tropics and the high-elevation alpine regions (Behera et al. 2002, Roy and Behera 2005), a study of endemism and species diversity in nearby Nepal reports that the highest proportion of endemic vascular plant species is found between 3800m and 4200m (Vetaas and Grytnes 2002).

Here, we analyze data on forest plots distributed throughout Arunachal Pradesh. Our study explores changes in diversity patterns across 291 belt transects established by researchers at the North Eastern Regional Institute of Science and Technology (NERIST) in Nirjuli, Arunachal Pradesh, from 2007 to 2010. The forest plots were initially designed to investigate the species richness in the region, but because the plots encompass a vast elevational span, these data provide a unique opportunity to also explore shifts in community structure and richness. We use phylogenetic and taxonomic measures of diversity as well as indices of phylogenetic dispersion in combination with a regional phylogeny to evaluate elevational trends in richness and phylogenetic diversity, and to identify phylogenetically distinct sites, which may point to the presence of evolutionarily distinct glacial relicts.

Methods

Study site

The forest plots were established throughout the north east province of Arunachal Pradesh, India (27.06°N, 93.37°E) by NERIST. Mountains in Arunachal Pradesh range in altitude from 200m to 7500m, spanning climates that vary from tropical to alpine.

The data include species identifications of the trees and shrubs found within 352 belt transects (referred to as plots herein). Plots range in elevation from 87m to 4090m above sea level, representing four distinct forest ecosystems: tropical evergreen/semi-evergreen, subtropical broadleaf/pine, temperate broadleaf/coniferous and alpine. Following preliminary examination of the data, several plots were excluded from the study, including those established in plantation fields or in fields without any tree or shrub species present, as noted by the field researchers. To the best of our knowledge, the 291 plots retained in the analysis represent natural forest with varying degrees of disturbance. Because of sampling practicalities, there was some variation in plot size (which ranged from 500m^2 to 5000m^2), we therefore divided the number of individuals of each species by total plot area, yielding the number of individuals per m^2. Furthermore, not all species were identified to species level, and this fraction varied among plots. We chose to analyze all 291 plots despite the differences in identification after determining that trends with elevation remained similar among groups of plots with differing percent identification (see Supplementary material Appendix 1, Table A1).

Phylogeny reconstruction

A molecular phylogeny was reconstructed for the tree species in the study using sequence information from Genbank. We used three plant DNA barcodes: rbcL, matK and ITS1 and 2, although all three barcodes were rarely available for the same species (Kress et al. 2005, Hollingsworth et al. 2009). When barcodes were not publically available on Genbank for a species but were available for a sister taxon sampled in our study, we included the sister taxon and added the missing species post-hoc as tip polytomies. If gene information was missing and a given species did not have a representative sister species in the phylogeny, we looked for sequences for another regionally occurring species from that genus (occurrence was based on Materials for the Flora of Arunachal Pradesh, Hajra et al. 2006). We were unable to locate information on congenerics for three species (*Balakata baccata*, *Khasiaclunea oligocephala*, and *Oxyspora paniculata*); we thus included these taxa as polytomies to their closest relatives present in the phylogeny (*Ostodes paniculata*, *Breonia oligocephala*, *Melastoma malabathricum* respectively) based on the APG3 phylogeny (Bremer et al. 2009). This iterative process allowed us to generate a DNA matrix for 206 of the 279 species in the regional pool. The final sequences used for constructing the phylogeny are included in Supplementary material Appendix 2 (Table A2).

Sequences were aligned using MAFFT ver.7 (Katoh and Standley 2013) and trimmed using BioEdit (Hall 1999). We concatenated the sequences using SequenceMatrix ver 1.7.8 (Vaidya et al. 2011) yielding a combined matrix 4365 bases in length. We inferred the phylogeny in MrBayes ver. 3.2.2 (Ronquist and Heulsenbeck 2003) by partitioning the data for each sequence and assigning the appropriate evolutionary model, as determined by modelTest in the *phangorn* R library (Schliep 2011). The genes rbcL, ITS1 and ITS2 were assigned the GTR+G+I model, while matK was assigned the GTR+G model. The phylogeny was constrained at the order or family level by assigning species to their known clades within MrBayes. We ran 25 million generations, and excluded the first 25% as burnin. One hundred phylogenies were randomly selected from the posterior distribution and rooted on the fern, *Angiopteris evecta*; each tree was then made proportional to time using calibration points on four nodes: root (454 mya; Clarke et al. 2011), Coniferae (309.5 mya; Clarke et al. 2011), Mesangiospermae (248.4 mya; Clarke et al. 2011), and Magnoliidae, Monocotyledoneae and Eudicotyledoneae (132 mya; Magallón et al.

2015). Missing taxa were included at this stage as polytomies, using taxonomy as a guide, with the function *add.species.to.genus()* from the R package phytools (Revell 2012). The resulting phylogenies thus include all 279 taxa from the region. All subsequent phylogenetic analyses were conducted on these 100 phylogenies. A sample phylogeny is included in Supplementary material Appendix 3 (Fig. A3).

Analysis of plant communities

For each plot we calculated: species richness, phylogenetic diversity (Faith 1992) and the net-relatedness index (Webb et al. 2002), using the R library *picante* (Kembel et al. 2010). We calculated both net phylogenetic diversity, which is equal to the sum of branch lengths represented in a community and the standardized effect size of phylogenetic diversity, which corrects for species richness with a tip-swap algorithm assuming the regional phylogeny (279 species) as the species pool. The net-relatedness index (NRI) incorporates evolutionary information from the phylogeny to calculate the average relatedness of species within a community relative to a null expectation of random community assembly. We calculated both abundance weighted and non-weighted NRI using the same null model as for standardized effect size of phylogenetic diversity. We used linear regression to explore how these metrics varied with elevation, which was normalized with a log transformation.

We next calculated two pairwise measures of beta diversity among plots. First, we used Sorenson's index to contrast species composition between plots using the *vegdist()* function from the *vegan* R library (Oksanen et al. 2007). Second, we used a phylogenetic equivalent of the Sorenson index to calculate phylogenetic beta diversity between plots using the *phylosor* function in *picante* (Bryant et al. 2008), which quantifies the proportion of shared branch lengths.

We then determined the local contributions to regional beta diversity (LCBD) using the method of Legendre and De Cáceres (2013). R-code for implementing this function is available from [http://adn.biol.umontreal.ca/~numericalecology/Rcode/]. This metric identifies plots with unique or unusual composition. LCBD also reports species contributions to beta diversity (SCBD) which identifies species with high abundances in relatively few sites (Legendre and De Cáceres 2013). Because we were also interested in phylogenetic patterns, we used a simple extension of this metric to estimate phylogenetically-informed LCBD (herein referred to as

PLCBD) by using the phylogenetic beta diversity distance matrix in place of the Euclidean distance matrix of species compositional dissimilarities (*phyloSor* outputs a similarity matrix which was converted to represent dissimilarities for this analysis). We did not calculate significance values for PLCBD due to the extensive computational requirements associated with iterating across 100 separate phylogenies, and we were more interested here in the overall patterns of PLCBD in the landscape rather than the statistical significance of any particular plot.

We explored structure in beta diversity by contrasting Sorenson's index with the phylogenetic equivalent, phylosor, and compared the distance decay in similarity from the plot with the lowest LCBD and the plot with the lowest PLCBD, respectively. This comparison allows us to examine whether taxa (tips) or lineages (branches) change more rapidly as we move from plots with low to high contribution to beta diversity. We also used partial-mantel tests to separately explore the relationship between phylogenetic beta diversity and distance (space) or elevation (environment). Finally, we explored the relationship between plot contributions to beta diversity, space and environment by modelling LCBD and PLCBD against the geographical distance and difference in elevation from the geographic center of the study site (Fig. 1).

All analyses were performed using R ver. 3.0.2. (R Core Team 2015).

Results

Overall patterns of diversity

Both species richness and phylogenetic diversity decreased with increasing elevation (SR: R^2_{adj}= 0.285, P<0.001; PD: R^2_{adj}= 0.215, P<0.001). Standardized effect size of PD also increased with elevation, but the relationship was weaker, and plots with significantly higher PD than expected were located throughout the landscape (Supplementary material Appendix 4). In addition we observed a significant, albeit weak, negative relationship between phylogenetic dispersion (indexed by NRI) and elevation (R^2_{adj}=0.133, P<0.001 and R^2_{adj}=0.132, P<0.001 for unweighted and weighted NRI, respectively). Thus, phylogenetically clustered communities were marginally more often found at low elevations and communities became increasingly over-dispersed at higher elevations, contrary to our initial hypotheses. We found the opposite relationships (non-weighted: R^2_{adj}=0.047, P<0.001; weighted: R^2_{adj}=0.039, P<0.001) when gymnosperms and ferns were removed from the analysis, although the relationships were even weaker (Supplementary

material Appendix 5, Fig. A5). The site with the lowest LCBD (least distinct community) was located near the geographical center of the study site (Fig 2a; 94.704E, 27.727N). The site with the lowest PLCBD was also fairly central, but slightly to the east (Fig 2b; 95.648E, 28.249N). Both sites were at relatively low elevations ($LCBD_{min}$=528m, $PLCBD_{min}$=295m).

In general, species turnover (Sorenson's Index) occurred at a faster rate than phylogenetic branch turnover (phylosor), as illustrated by the compositional decay from the site with lowest LCBD (Fig. 3a; slope=0.66, R^2_{adj}=0.745) and the site with lowest PLCBD (Fig. 3b; slope=0.67, R^2_{adj}=0.687), respectively. A mantel test of the Sorenson's dissimilarity matrix and the phylosor dissimilarity matrix (transformed to dissimilarity by subtracting from one) revealed a strong relationship between the pairwise metrics (mantel r=0.703, *P*=0.001). We observed a strong relationship between phylogenetic beta diversity and elevation (mantel r=-0.4638, *P*<0.001), which remained significant when we corrected for differences in geographical distance among plots (partial mantel r=-0.38, *P*<0.001) and when gymnosperms and ferns were removed from the analyses (Supplementary material Appendix 6, Table A6).

The relationships between PD, NRI and phylogenetic beta diversity with elevation was not sensitive to the proportion of individuals identified per plot (Supplementary material Appendix 1, Table A1).

Local contributions & distance decay (within a center of endemism)

Local contributions to beta diversity (LCBD), although not phylogenetically informed, provided some insight into the structuring of communities. Plots located on the periphery of study area tended to have higher contributions to beta diversity than plots in central, low-elevational sites (Fig. 2a). We found a weak, but significant, relationship between the strength of contribution and elevation, with plots contributing more at higher elevations (Table 1, Fig. 2a). A similar trend was found for phylogenetic local contribution to beta diversity (PLCBD; Table 1, Fig. 2b). The relatively low r-squared can, in part, be explained by the triangular relationship in the data, with plots at lower elevations having higher variance in their contribution.

LCBD was significantly correlated with both distance and difference in elevation from the geographical center of the study site, with distance the stronger predictor (Table 1). The equivalent correlation with elevation for PLCBD was weaker (excluding plots with a species

richness of one), and in contrast to results with LCBD, elevation was the better predictor (Table 1). The taxa which contributed the most to beta diversity, as indexed by the species contribution to beta diversity (SCBD; Legendre and De Caceres 2013), were *Castanopsis indica*, *Duabanga grandiflora, Pinus roxburghii*, and *Quercus sp.*; these taxa are restricted in their distribution but have high local abundances. The distribution of both LCBD and PLCBD was qualitatively similar when gymnosperms and ferns were removed from the analyses (Spearmann rank correlations; LCBD=0.939, PLCBD=0.853).

Discussion

We explored shifts in tree community structure and richness across one of the largest elevation gradients in the world, the Himalayas of Arunachal Pradesh, India. We found that species richness and phylogenetic diversity declined with elevation, a result that is consistent with our predictions and existing ecological theory. In general, elevational declines in richness are hypothesized to be due to factors similar to those driving the decline observed along the latitudinal gradient, such as the reduced availability of resources, colder temperatures and increased extinction rates at regional scales (Lomolino 2001, McCain and Grytnes 2010). A reduction of resources (lush soils and nutrients, for example) and colder temperatures at high elevations can limit the number of individuals and select for species with specific niche attributes (McCain and Grytnes 2010), with only those species possessing the appropriate traits and adaptations able to establish and thrive in these environments.

Several lines of evidence in our study suggest that environmental filtering is contributing to shifts in community structure with elevation; including high local endemism and rapid phylogenetic turnover that was more strongly tied to changes in elevation than with distance. However, one key metric used to infer filtering, the net-relatedness index, which describes the phylogenetic dispersion of lineages (Webb et al. 2002), did not reveal a strong pattern with elevation. We suggest two possible explanations for the lack of pronounced community phylogenetic structuring along the elevational gradient despite strong species filtering. First, important traits could demonstrate convergent evolution, such that distant relatives share similar ecological habitats. Second, in high montane regions, filtering may operate on evolutionary distinct glacial relicts, remnants of once more diverse cold-adapted clades. Much previous work has focused on the former (Jobbágy and Jackson 2000, Kraft et al. 2007 (simulations), Losos

2011, Read et al. 2014); here we explore the latter, and consider the phylogenetic evidence for glacial relicts structuring communities in the high elevations of the Himalayas.

Areas of high topographic relief such as mountain ranges have been linked to the presence of glacial refugia (Weber et al. 2014) because they provide cooler, more stable climates during warming periods (Stewart et al. 2010). These refugia provide suitable conditions for species that have retreated to microclimates resembling those of the last glacial maxima (Vetaas and Grytnes 2002, Ohlemüller et al. 2008). Such refugia might be increasingly important for many species given current warming trends (Opgenoorth et al. 2010). However, relict communities or species are a challenge to identify, usually requiring detailed population genetics on a regional scale, allowing past patterns of migration to be reconstructed (Hampe et al. 2003, Petit et al. 2005, Vargas 2007).

Our approach combines knowledge on the evolutionary relationships among species with information on shifts in community composition and allows us to identify diversity patterns that might reflect the distribution of relict lineages and glacial refugia. For example, glacial relicts could represent survivors from once more diverse clades, perhaps a result of higher extinction rates of related species (Cain 1944, Fryxell 1962, Brooks and Bandoni 1988). Therefore, the communities in which they are found may be more phylogenetically diverse relative to their species richness. Because glacial relicts also tend to be range restricted (Habel and Assmann 2009) we expect that relicts would also contribute more to the overall beta diversity of a region. Although we did not find strong evidence for higher phylogenetic diversity within higher elevation plots in Arunachal Pradesh, likely because both richness and phylogenetic diversity tend to decrease with elevation, we show high species and phylogenetic turnover, supporting evidence for high local endemism in the region.

Investigating phylogenetic beta diversity in addition to species beta diversity provides added information on evolutionary history and corrects for species non-independence (Graham and Fine 2008). We found that species turnover occurred at a faster rate than branch turnover throughout the landscape; this pattern and the strong relationship between the two indices would be expected under null expectations. Previous work has interpreted higher species turnover as evidence for niche conservatism plus environmental filtering (Jin et al. 2015). However, phylogenetic clustering among species should also be expected with high conservatism and

strong filtering, which we did not observe. We therefore more carefully explored patterns of phylogenetic beta diversity, investigating the relative rates of turnover in branches with space versus elevation (our proxy for environment).

Our results demonstrate that turnover of clade membership occurs along the elevational gradient, independently from turnover occurring with geographical distance, echoing the findings of Gonzalez-Caro et al. (2013), which showed that beta diversity in a tropical mountain system was not related to distance, but to temperature which varies with elevation (McCain and Grytnes 2010). We suggest that general high phylogenetic beta diversity, the strong correlation between phylogenetic beta diversity and elevation, as well as the lack of clear patterns of species relatedness indicates environmental filtering of small ranged, evolutionary distinct, taxa. We propose that these taxa might represent glacial relicts or refuge species.

The presence of glacial relicts would not only disrupt patterns of phylogenetic clustering predicted at high elevations in strongly filtered communities, but also contribute to the uniqueness or beta diversity of those communities. We show that high elevation plots do indeed contribute disproportionately to regional beta diversity. Because highly contributing plots represent those that contain communities with relatively greater species uniqueness (Legendre and De Cáceres 2013), they might also reflect the presence of narrow ranged and evolutionarily distinct endemics. Species with high individual contributions, many of which are endemic to the region, include *Pinus roxburghii* (Puri et al. 2011, IUCN RedList 2015), *Pinus wallichiana* (Saqib et al. 2013, IUCN RedList 2015) and *Livistona jenkinsiana* (Sikarwar et al. 2000). Both environment and distance from the center of the study site were important predictors of contributions to species beta diversity, indicating that communities are increasingly unique across space and elevation. In contrast, phylogenetic contributions to beta diversity increased more strongly with elevation than with distance, indicating that high elevation plots represent more phylogenetically unique clades. We suggest that the weaker relationship between distance and phylogenetic contributions to beta diversity might indicate that dispersal limitation may be less important in our study system. While dispersal limitation has been shown to stabilize centers of endemism (Weber et al. 2014), it does not appear to have a significant effect on local tree community structure in Arunachal Pradesh, despite the high proportion of endemics in the region.

Given strong filtering, high elevation taxa are likely well adapted to the environmental conditions where they are found; some of these species may have retreated to higher, colder, altitudes following the last glacial maximum. The absence of strong signal in phylogenetic clustering indicates that these taxa do not, however, represent radiations within one or a few clades, instead they may represent remnants from formerly more diverse clades in the region.

A better understanding of richness patterns ultimately requires researchers to collect data in isolated, overlooked, and hard to access regions around the world. We suggest that regions with unique species, high endemicity and distinct geography should become priorities for research and conservation. By understanding the historical factors that have shaped them, these communities might provide insights into responses to future environmental change, not at the individual species level, but at the level of the ecological assemblage. Through the use of community-level diversity indices, we showed that filtering strongly drives community structure across elevations, and we suggest that some high-elevation communities may represent refugia for glacial relicts. High altitude refugia may be important conservation targets because they can provide an escape from generally increasing temperatures globally by matching to the cooler climates resembling the conditions under which many taxa may have evolved.

PART III: Conclusions and Future Research

The field of community phylogenetics has grown rapidly in a short time. Phylogenetic methods not only provide insight into the potential biotic and abiotic processes structuring communities but also allow us to account for the relatedness (and non-independence) of species. Species richness patterns provide only limited insight into the multitude of factors that structure biodiversity patterns. Using phylogeny we can infer process from pattern by factoring evolutionary history into analyses of diversity and dispersion. Here I explored multiple diversity metrics that capture information on both richness and phylogenetic composition to investigate the community assembly of forest trees in the Himalayas of Arunachal Pradesh, India.

Revisiting objectives

The forests of Arunachal Pradesh are species rich and diverse, changing notably across the landscape. Although many studies on species diversity have been conducted in the region, community-level diversity patterns have been largely overlooked, perhaps due to the challenges in sampling species rich regions with difficult terrain. The researchers at NERIST have been able to provide a detailed, high resolution dataset with which more specific questions of diversity and richness patterns can be addressed. We find that species richness and phylogenetic diversity decreased with elevation, but that species relatedness did not vary strongly. The decrease in species richness with elevation and latitude is well documented in the literature; however, community-level patterns and trends in phylogenetic structure are less well understood. Nevertheless, this information is useful in the context of conservation and restoration (more on this below) and for improving our understanding of the mechanisms structuring species richness gradients, especially within remote, poorly studied, regions where we lack detailed knowledge of species ecologies.

We have suggested that environmental filtering plays an important role in structuring forest communities along the vast elevational gradient in Arunachal Pradesh. Although this conclusion may not seem surprising, the patterns reported in the literature are not always consistent with prior expectations. For instance, environmental filtering may occur without

leading to a clear pattern of phylogenetic structuring, and no one metric can definitively conclude process from pattern. We drew inference by combining results on taxonomic and phylogenetic diversity and turnover (beta diversity), as well as plot level contributions to beta diversity. We found that phylogenetic beta diversity among plots varied more strongly with elevation than distance, but that species turnover more quickly than branches. In addition, plots that contributed more to the overall beta diversity of the region tended to be those furthest from the center of the study site. Together these patterns suggest that habitat heterogeneity might drive rapid turnover in species and branches, and that unique species communities are maintained at higher elevations. Our results provide strong evidence for environmental filtering, even though we did not detect significant trends in phylogenetic clustering.

By integrating new metrics with phylogeny, we were able to reveal that plots at higher elevations contribute more to both species and phylogenetic beta diversity. These sites contain species or lineages that are high in abundance but have restricted distributions. We suggest that these plots may represent high elevation refugia, or areas where cold-adapted species can persist. The presence of these evolutionarily distinct taxa in higher elevational sites may also be part of the explanation for why we do not find strong evidence for phylogenetic clustering at high elevations.

Our findings have important implications for conservation prioritization in light of changing climates and increased anthropogenic pressures globally. Anthropogenic pressures in Arunachal Pradesh are high and projected to increase, as the forests provide several ecosystem services (timber, food, medicine) to the local communities (Menon et al. 2001). As a result, deforestation is commonplace and impacts may be particularly severe where the forest is easily accessed from towns and roads. With rising global temperatures, tree species will be exposed to additional stresses. For example, recent studies have shown that species are migrating northward or upwards to remain within their optimal niche envelope (Lenoir et al. 2008, Morueta-Holme et al. 2015). The impact of both anthropogenic pressures and changing climates is not clear at the community level. Our study suggests that forest community composition is strongly structured by the environment. Environmental change is thus likely to impact forest communities. These changes may, in turn, impact the resources that forests provide to local inhabitants.

Phylogenetic diversity may be a useful metric for conservation prioritization because it can help identify lineages and communities that contain the most functional diversity. Thus, identifying taxonomically and phylogenetically distinct communities can help inform conservation prioritization. We have shown that phylogenetically distinct communities are located at high elevations, and are thus less likely to be exploited by local habitants, but they may be subject to higher stress from climate change. If species alter their ranges to adjust for warming temperatures, these cool, high elevation sites might provide important refugia for temperature-sensitive species.

Future Research

Future work could incorporate species distribution modelling to characterize the climate niches of high elevation species. With these models, species ranges could be mapped and overlapped to identify potential barriers to dispersal, and sites with rare or contracting environments. High resolution environmental data such as humidity, rainfall, temperature and soil composition will be essential for generating such models, but are often lacking at the appropriate scale for this region, where very large changes in elevation, slope and aspect can result in very different environmental regimes over short spatial distances.

We should additionally strive to collect additional data on species' functional traits. Although one of the benefits of phylogenetics is the ease with which it can be incorporated into studies lacking trait data, the various phylogenetic metrics can be improved with additional functional trait information. Collecting trait information is time consuming and difficult work, especially for a study of this size, but could provide additional insight into community structuring. For example, with detailed trait information, it would be possible to test for convergent evolution and to more directly evaluate evidence for trait dispersion. While phylogeny might provide a useful proxy for expected ecological similarity among species, detailed trait data is critical for identifying the specific selective forces structuring species distributions and co-existence.

With an increased need for richness and conservation assessment throughout the world, phylogenetic community ecology can provide an additional perspective on how (and sometimes why) communities are presently structured, as well as how they might adapt to projected environmental change. Fortunately, the tools required to build phylogenies and to compute

phylogenetic metrics are becoming easier to use and more widely available. Trait and species richness information can complement phylogenetic approaches—but neither approach may be sufficient on its own. While phylogenetic methods are constrained by various assumptions, they can begin to account for species non-independence and evolutionary history in analyses of diversity patterns, and, as I have shown here, potentially identify regions for conservation based on unique phylogenetic structure. The work presented in this thesis indicates that Arunachal Pradesh contains phylogenetically unique forests that potentially have a high conservation value, both in terms of genetic diversity and resource availability for local human populations.

Figures

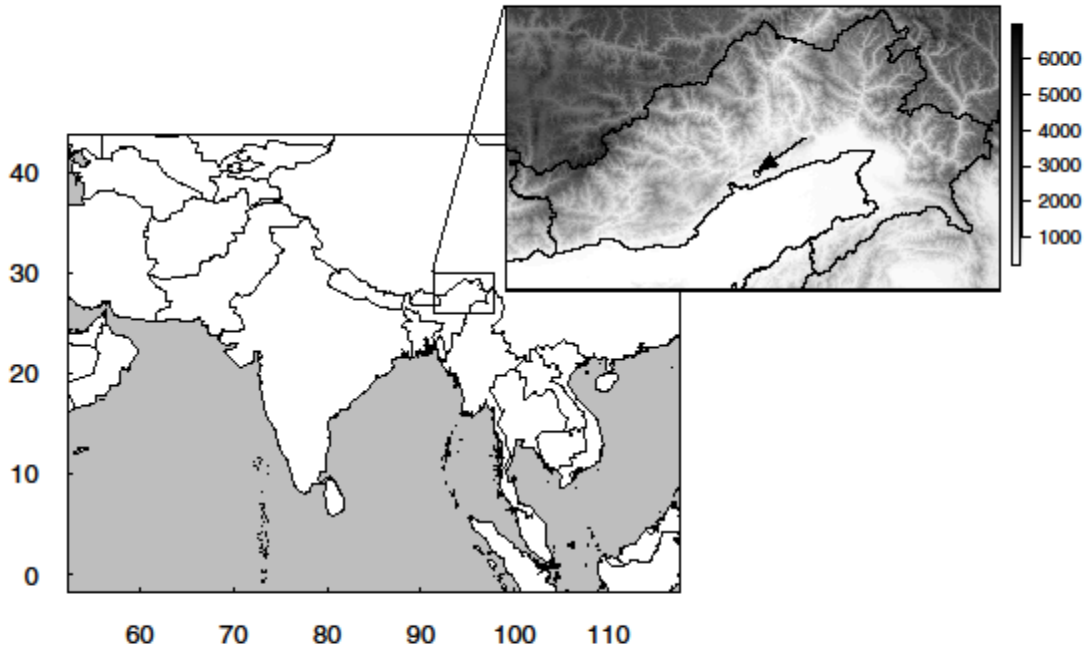

Figure 1: Map of the study site in Arunachal Pradesh, India, with darker shading indicating higher elevations. The sites in our study range in elevation from 87m to 4090m above sea level. The geographic center of the study is identified with an arrow in the inset figure (94.704E, 27.727N, elevation: 709m).

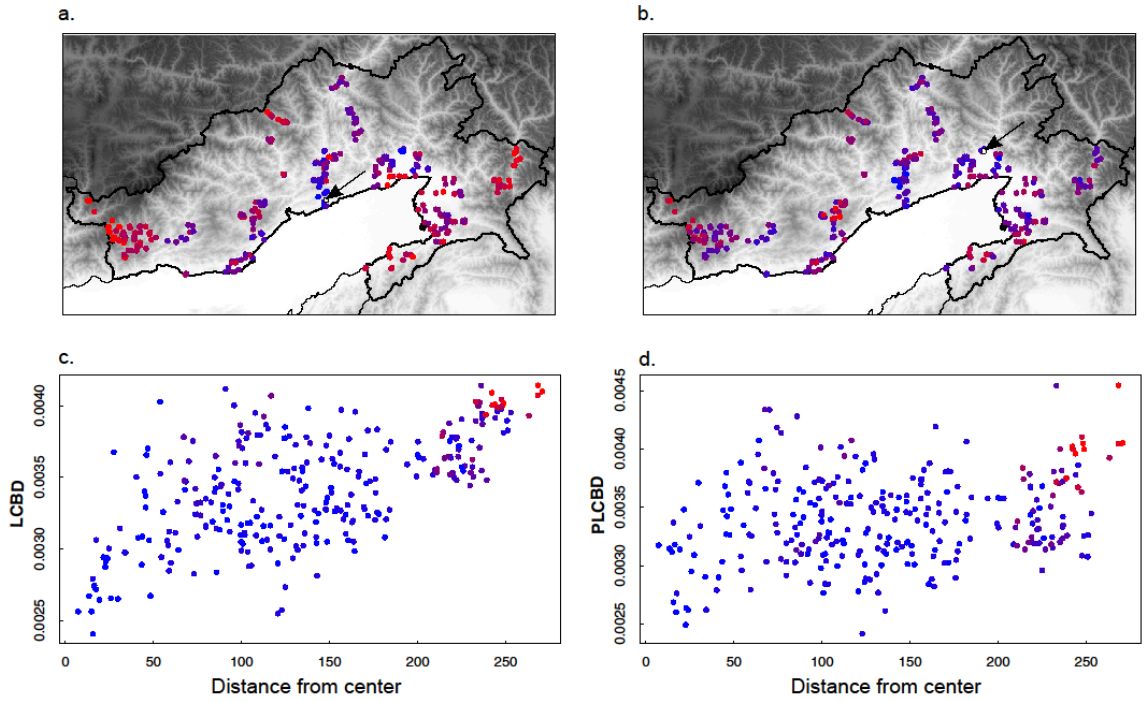

Figure 2: Maps show the spatial distribution of LCBD (a) and PLCBD (b). For (a) and (b), symbols are shaded by contribution, where red indicates higher contributions to beta diversity. The plots with the lowest contributions are colored white and identified with arrows. These plots represent the least unique sites for LCBD (a) and PLCBD (b), respectively. We also show the change in local contribution to beta diversity (LCBD; Fig. 2c) and local contribution to phylogenetic beta diversity (PLCBD; Fig. 2d) of each plot with increasing distance from the geographical center of the study site (see Fig. 1). Here, symbols are shaded by elevational differences, where red indicates a large difference in elevation from the center of the site and blue indicates small differences.

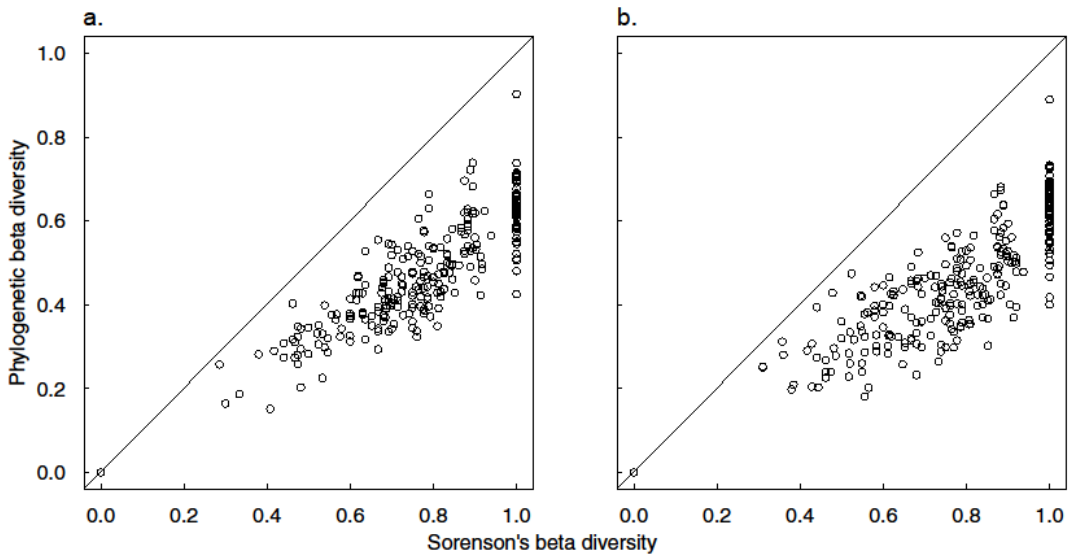

Figure 3: The relationship between phylogenetic beta diversity and Sorenson's beta diversity from the site with lowest LCBD (a) and the site with lowest PLCBD (b). Both phylogenetic and Sorenson's beta diversity are represented on a scale from 0 to 1, where 0 indicates sites that are compositionally identical and 1 indicates no overlap between sites in either phylogenetic branch lengths or taxa, respectively.

Tables

Table 1: Linear models testing change in LCBD and PLCBD with elevation and distance. Distance represents the geographical distance between each plot and the geographical center of the study site while elevation is the absolute value of the difference in elevation between each plot and the center of the study site (709m).

Model	$R^2_{adjusted}$	P_{model}	$P_{distance}$	$P_{elevation}$
LCBD				
Elevation	0.276	<0.001		
Distance + elevation	0.4307	<0.001	<0.001	<0.001
PLCBD				
Elevation	0.1628	<0.001		
Distance + elevation	0.1666	<0.001	0.456	<0.001

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Supplementary Material

Appendix 1: Assessing sensitivity of results to differences in species identification among plots.

Areas of high diversity, although ecologically invaluable, pose a unique challenge for researchers. Species identification is highly related to the knowledge of the field personnel and researchers involved (Elliott and Davies 2014). As such, not all individual trees in our study were identified to the genus level. To determine whether the discrepancy among plots (in terms of species identification) had any effect on the overall patterns we observed, we separated our data into three groups: all 291 plots used in the study, plots with at least 50% of individuals identified to genus level (257 plots), and plots with at least 75% of individuals identified to genus level (174 plots).

Using the same 100 phylogenies as for all other analyses, we calculated phylogenetic diversity (PD), the non-abundance weighted net-relatedness index (NRI) and phylogenetic beta diversity (PBD) for the three groups of plots, defined above. We regressed PD and NRI for each group with log-transformed elevation and calculated mantel tests for pairwise phylogenetic beta diversity and pairwise elevation or distance. We found that the patterns we observed in the study were conserved for all groups, suggesting that using all plots, despite varying levels of species non-identification does not affect general patterns of phylogenetically informed indices along the elevational gradient and overall landscape (Table A1). Phylogenetic metrics such as PD, NRI and PBD are calculated as standardized effect sizes using 1000 null iterations each, which corrects for differences in species richness (higher richness with elevation) at the plot level. Moreover, these metrics consider evolutionary information maintained in the branch lengths and adding or removing taxa (phylogenetic tips) may not add significant evolutionary information or alter the overall patterns observed.

Table A1: Regressions for both PD and NRI against log-transformed elevation for three groups of plots (all plots, at least 50% identified, at least 75% identified). We also include the results from mantel tests for distance matrices of phylogenetic beta diversity, elevational differences and distance.

Linear models

Model	R^2_{adj}	*P*	F	DF
PD~elevation				
All plots (291)	0.198	<0.001	72.82	289
50% identified (257)	0.198	<0.001	64.31	255
75% identified (174)	0.208	<0.001	46.47	172
NRI~elevation				
All plots (291)	0.133	<0.001	44.83	285
50% identified (257)	0.192	<0.001	60.87	251
75% identified (174)	0.251	<0.001	57.56	168

Mantel Test

Model	mantel-r	*P*
PBD~elevation (mantel)		
All plots (291)	-0.4638	0.001
50% identified (257)	-0.4767	0.001
75% identified (174)	-0.4473	0.001
PBD~distance (mantel)		
All plots (291)	-0.312	0.001

50% identified (257)	-0.3412	0.001
75% identified (174)	-0.3575	0.001

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Appendix 2: Genbank accession numbers for phylogeny reconstruction.

Table A2: List of accession numbers used to reconstruct the 100 phylogenies used in the study. In some cases, sequences were not available for the species in our study and we used sequences for closely related species. Both the species names for the sequences and the name used in the phylogenies are noted.

GenBank species name	MATK	RBCL	ITS1-2	Name in phylogeny
Abies alba	HQ619823.1	FR831929.1		Abies alba
Abroma augusta	HM488448.1	AJ012208.1	AJ277462.1	Abroma augusta
Acacia catechu	AF274141.1	GQ436355.1	KC952019.1	Acacia sp.
Acer caesium		DQ978397.1		Acer caesium
Acer campbellii	JF952995.1	DQ978398.1	HM352652.1	Acer campbellii
Acer cappadocicum			AJ634579.1	Acer cappadocicum
Actinodaphne obovata	AF244410.1		AY265398.1	Actinodaphne obovata
Aglaia elaeagnoidea	AB925001.1	AB925482.1	AY695536.2	Aglaia spectabilis
Ailanthus integrifolia	EU042843.1	JF738642.1		Ailanthus integrifolia
Alangium chinense	FJ644642.1	L11209.2	FJ610017.1	Alangium chinense
Albizia lebbeck	JX495667.1	KC417043.1		Albizia lebbeck
Albizia lucidior			JX856396.1	Albizia lucidior
Albizia procera	KC689800.1	KC417044.1	JX856397.1	Albizia procera
Alnus nepalensis	JF953073.1	FJ844581.1	AJ251676.1	Alnus nepalensis
Alsophila spinulosa		AB574756.1		Cyathea spinulosa
Alstonia scholaris	Z70189.1	X91760.1	DQ358880.1	Alstonia scholaris
Altingia excelsa	AF013037.1	AJ131769.1	AF304525.1	Altingia excelsa
Angiopteris evecta		EU439092.1		Angiopteris evecta
Aquilaria sinensis	HQ415244.1	GQ436619.1	KF636364.1	Aquilaria malaccensis
Aralia cachemirica			AY725107.1	Aralia sp
Ardisia crenata	GU135103.1	GU135270.1	JF416242.1	Ardisia macrocarpa
Artocarpus chama	AB924725.1	AB925336.1	FJ917047.1	Artocarpus chama
Artocarpus heterophyllus		JX856635.1	FJ917039.1	Artocarpus heterophyllus
Azadirachta indica	EF489115.1	AJ402917.1	AY695594.1	Azadirachta indica
Baccaurea lanceolata	AY552419.1			Baccaurea ramiflora
Bambusa balcooa	JX966236.1		EU244594.1	Bambusa balcooa

Bambusa tulda	EU434248.1		EF540854.1	Bambusa tulda
Bauhinia ungulata	JQ587517.1	JQ591586.1	FJ009818.1	Bauhinia ungulata
Beilschmiedia roxburghiana	AB924825.1	AB925437.1		Beilschmiedia fagifolia
Berberis asiatica	GU934752.1	GU934836.1	GU934647.1	Berberis leschenaultii
Bhesa robusta	AB925166.1	AY935723.1		Bhesa robusta
Bischofia javanica	EF135508.1	AY663571.1		Bischofia javanica
Boehmeria glomerulifera		KF138115.1	KF137807.1	Boehmeria glomerulifera
Boehmeria macrophylla	KF137956.1	JF317496.1	KF835865.1	Boehmeria macrophylla
Boehmeria nivea	KF137957.1	AJ235801.1	KF835885.1	Boehmeria nivea
Boehmeria platyphylla			KF835876.1	Boehmeria platyphylla
Boehmeria rugulosa	KF137960.1	KF138125.1	KF137817.1	Boehmeria rugulosa
Bombax ceiba	JX495673.1	JN114787.1	HQ658377.1	Bombax ceiba
Brassaiopsis hispida		JQ933245.1	AY725117.1	Brassaiopsis mitis
Breonia chinensis		AJ346968.1	AJ346858.1	Breonia chinensis
Bridelia retusa	HQ415363.1		FJ439910.1	Bridelia retusa
Brucea javanica	AB924837.1	EU042986.1	AY510155.1	Brucea javanica
Calamus erectus	JQ041983.1	JQ042035.1		Calamus sp
Callicarpa arborea	FM163260.1	JF738395.1	FM163241.1	Callicarpa arborea
Callicarpa macrophylla	FM163273.1	JQ618476.1	FM163246.1	Callicarpa macrophylla
Camellia sinensis	AF380077.1	AF380037.1	EU579774.1	Camellia sinensis
Canarium strictum		FJ466638.1		Canarium strictum
Carallia brachiata	AF105086.1	AB925477.1	AF328957.1	Carallia brachiata
Caryota urens	JF344998.1	JQ734494.1	JF344933.1	Caryota urens
Casearia glomerata	HQ415293.1			Casearia vareca
Cassia fistula	JQ301870.1	JX571794.1	JX856432.1	Cassia fistula
Castanopsis indica	JF953474.1	JF941185.1	AY040377.1	Castanopsis indica
Casuarina stricta	U92858.1			Casuarina sp
Chukrasia tabularis	AB924866.1	AB925481.1	FJ518894.1	Chukrasia tabularis
Cinnamomum bejolghota	GQ248098.1	GQ248569.1		Cinnamomum bejolghota
Citrus maxima	AB626794.1	GQ436734.1	AB673398.1	Citrus maxima
Citrus reticulata	FJ716729.1	JQ593913.1	AB456115.1	Citrus reticulata
Clerodendrum infortunatum		JQ724863.1		Clerodendrum infortunatum
Cordia africana		KF158134.1		Cordia grandis

Coriaria nepalensis	KF022395.1	KF022461.1	KF022334.1	Coriaria nepalensis
Cornus capitata	DQ341340.1	AY530926.1	AY530915.1	Cornus capitata
Cupressus torulosa	HM023995.1	AY988257.1	AY988393.1	Cupressus torulosa
Cyathea podophylla	JF303907.1			Cyathea sp
Cyathea klossi		EU352299.1		Cyathea sp
Dalbergia sissoo	AF203582.1	JX571817.1	EF451079.1	Dalbergia sissoo
Daphne laureola	HM850899.1	JN892035.1	GQ167536.2	Daphne papyracea
Debregeasia saeneb	JF317422.1	JF317481.1	KF137835.1	Debregeasia saeneb
Dendrocalamus hamiltonii	HM448942.1			Dendrocalamus hamiltonii
Dillenia indica	AB924752.1	FJ860350.1	AY096030.1	Dillenia indica
Dipterocarpus retusus	KF021568.1			Dipterocarpus retusus
Docynia indica	JQ391000.1	JQ933307.1	JQ392426.1	Docynia indica
Duabanga grandiflora	GQ434087.1	AY036150.1	AF163695.1	Duabanga grandiflora
Dysoxylum binectariferum	JX982143.1	JX982144.1	JX982145.1	Dysoxylum binectariferum
Elaeagnus umbellata	AY257529.1	HM849968.1	AF440257.1	Elaeagnus parvifolia
Elaeocarpus sphaericus		AF206765.1	DQ499079.1	Elaeocarpus floribundus
Elatostema acuminatum		AY208702.1		Elatostema platyphyllum
Engelhardia fenzelii	AY147099.1	AY147095.1	KF201317.1	Engelhardia spicata
Erythrina lanceolata	JQ587635.1	JQ591753.1		Erythrina stricta
Eucalyptus tereticornis			AF390482.1	Eucalyptus sp.
Eurya acuminata			AY626852.1	Eurya acuminata
Eurya japonica	AF380081.1	Z80207.1	AY626867.1	Eurya japonica
Exbucklandia populnea	U77092.1	AF081071.1	AF127504.1	Exbucklandia populnea
Ficus auriculata	JQ773629.1	JQ773648.1	JQ773837.1	Ficus auriculata
Ficus benjamina	JQ773507.1	JX571829.1	JQ773842.1	Ficus benjamina var. nuda
Ficus cyrtophylla	JF953730.1	JF941526.1	JQ773858.1	Ficus cyrtophylla
Ficus glaberrima	JF953733.1	JF941532.1	JQ773885.1	Ficus glaberrima
Ficus hirta	HQ415330.1	JQ773693.1	JQ773900.1	Ficus hirta
Ficus hispida	KC508602.1	GU935070.1	JQ773905.1	Ficus hispida
Ficus racemosa	GU935040.1	JF941550.1	HM368196.1	Ficus racemosa
Ficus semicordata	JQ773468.1	JF941553.1	JQ773985.1	Ficus semicordata
Garcinia cowa	HQ331596.1	HQ332054.1	AB110799.1	Garcinia cowa
Garcinia pedunculata		KF783274.1		Garcinia pedunculata

Garuga floribunda		GU246039.1		Garuga pinnata
Gaultheria trichophylla	JF953858.1	JF941732.1	HM597327.1	Gaultheria sp.
Gleditsia triacanthos	AY386849.1	JX572626.1	AF509981.1	Gleditsia assamica
Glochidion nomorale	AY936569.1			Glochidion heymeanum
Glochidion puberum		AY663586.1		Glochidion heymeanum
Gmelina arborea	JQ589430.1	KF381143.1		Gmelina arborea
Grewia glabra		JF738370.1		Grewia optiva
Gymnocladus chinensis	AY386928.2		AF510034.1	Gymnocladus assamicus
Heteropanax fragrans		JQ933360.1	JX106276.1	Heteropanax fragrans
Hevea brasiliensis	HQ606140.1		AB441762.1	Hevea brasiliensis
Hovenia dulcis	JX495724.1	JX571848.1	DQ146607.1	Hovenia dulcis var. dulcis
Hydrangea anomala	GU369710.1	JF941956.1	JF976652.1	Hydrangea sp.
Illicium verum	GQ434033.1	JQ003520.1	AF163724.1	Illicium griffithii
Juglans regia	HE966942.1	HE963521.1	HE574833.1	Juglans regia
Juniperus chinensis	JQ512420.1		EU243566.1	Juniperus sp.
Kydia calycina	EF207261.1			Kydia calycina
Lagerstroemia speciosa		JN114813.1	AF163696.1	Lagerstroemia speciosa
Leea macrophylla			JN160927.1	Leea macrophylla
Lindera glauca	AB442056.1	HM019477.1	AB500616.1	Lindera sp.
Litsea cubeba	AB259073.1	KF912878.1	AB260863.1	Litsea cubeba
Litsea monopetala	HM019346.1	HM019486.1	DQ120602.1	Litsea monopetala
Litsea salicifolia	KF523364.1	KF523365.1		Litsea salicifolia
Livistona jenkinsiana	HQ720190.1			Livistona jenkinsiana
Loranthus europaeus	EU544436.1			Loranthus sp
Loranthus delavayi		HQ317767.1		Loranthus sp
Lyonia ovalifolia	U61305.1	AF124580.1		Lyonia ovalifolia
Macaranga denticulata			AJ275630.1	Macaranga denticulata
Machilus gamblei	JF954542.1	JF942458.1	JF976983.2	Machilus kurzii
Maesa indica			JQ436585.1	Maesa indica
Magnolia hodgsonii	JN050055.1			Magnolia hodgsonii
Magnolia pealiana	AY008979.1	AY008901.1		Magnolia pealiana
Mallotus philippensis	HQ415385.1	GU441775.1	DQ866614.1	Mallotus philippensis
Mangifera indica	JQ586472.1	JF739088.1	AB071671.1	Mangifera indica

Melastoma malabathricum		AF270748.1	GQ265880.1	Melastoma malabathricum
Melia azedarach	EF489117.1	JX856725.1	AY695595.1	Melia azedarach
Merrilliopanax listeri			KC952369.1	Merrilliopanax alpinus
Mesua ferrea	HQ331661.1	GQ436685.1	AY625635.1	Mesua ferrea
Meyna tetraphylla			AJ315083.1	Meyna laxiflora
Michelia champaca		AY008902.1		Michelia champaca
Micromelum integerrimum			JX144208.1	Micromelum integerrimum
Moringa oleifera	JX092021.1	JX571866.1	AF378589.1	Moringa oleifera
Morus macroura	GU145567.1	GU145581.1	AB604232.1	Morus laevigata
Musa acuminata	KC904699.1	FJ871828.1	JF977066.1	Musa sp.
Myrica esculenta			FJ469994.1	Myrica esculenta
Oroxylum indicum	GQ434292.1	JN407262.1	FJ606747.1	Oroxylum indicum
Ostodes paniculata	EF135574.1	AJ402979.1		Ostodes paniculata
Pandanus tectorius	JX903664.1	M91632.1	EU816709.1	Pandanus furcatus
Persea bombycina		EU128737.1		Persea odoratissima
Phlogacanthus thyrsiflorus			EU528907.1	Phlogacanthus thyrsiflorus
Phoebe lanceolata	AB924934.1	AB925556.1	FM957844.1	Phoebe cooperiana
Phyllanthus emblica	FJ235251.1	AB925416.1	AB550082.1	Phyllanthus emblica
Pieris formosa	U61303.2	AF124581.1	EU547690.1	Pieris formosa
Pinus kesiya	AB161008.1	JN039276.1	AF037004.1	Pinus kesiya
Pinus merkusii	AY497287.1	AB019811.1	AF037006.1	Pinus merkusii
Pinus roxburghii	AB084495.1	JN854162.1	AF037021.1	Pinus roxburghii
Pinus wallichiana	JN854154.1	X58131.1	AF036991.1	Pinus wallichiana
Podocarpus neriifolius	KF713737.1	AF249618.1	KF713961.1	Podocarpus neriifolius
Prunus cerasoides	HQ235127.1	HQ235411.1	JQ034160.1	Prunus cerasoides
Psidium guajava	JQ588510.1	JQ592981.1	AB354956.1	Psidium guajava
Pterospermum acerifolium	KJ510943.1		JX856493.1	Pterospermum acerifolium
Pterospermum lanceifolium	AB924689.1	HQ415058.1	JX856596.1	Pterospermum lanceifolium
Pyrus communis	JN895841.1	JQ391382.1	JQ392467.1	Pyrus communis
Quercus baloot	HE583734.1		HE591363.1	Quercus baloot
Quercus glauca	JX860839.1	AB060571.1	HE611290.1	Quercus glauca
Quercus leucotrichophora	JX860844.1			Quercus leucotrichophora
Rhododendron arboreum	JF955906.1	JF943838.1	JF978202.1	Rhododendron arboreum

Rhododendron barbatum	EU087304.1			Rhododendron barbatum
Rhododendron cinnabarinum		JF943863.1	JF978227.1	Rhododendron cinnabarinum
Rhododendron falconeri	U61343.1			Rhododendron falconeri
Rhododendron fulgens	EU087314.1			Rhododendron fulgens
Rhododendron grande	U61336.1	GU176646.1	GU176633.1	Rhododendron grande
Rhododendron lanatum	EU087332.1			Rhododendron lanatum
Rhododendron maddenii	JF956017.1	JF943959.1	AY877281.1	Rhododendron maddenii
Rhododendron thomsonii	EU087359.1			Rhododendron thomsonii
Rhododendron wallichii	JF956143.1	JF944100.1	JF978451.1	Rhododendron wallichii
Rhus chinensis			EF682845.1	Rhus chinensis
Ricinus communis	GU134993.1	GU135207.1	AY918198.1	Ricinus communis
Sambucus adnata	JF956193.1	JF944171.1	JF978510.1	Sambucus adnata
Sarcochlamys pulcherrima		KF138244.1	KF137924.1	Sarcochlamys pulcherrima
Saurauia nepaulensis		Z83147.1		Saurauia nepaulensis
Schefflera venulosa			JF284828.1	Schefflera venulosa
Schima khasiana			HM100439.1	Schima khasiana
Schima wallichii	AF380100.1	AF380056.1	HM100444.1	Schima wallichii
Senna siamea	GU942496.1	JQ301862.1	KC984644.1	Senna siamea
Shorea assamica	AB246453.1			Shorea assamica
Shorea robusta		JX856763.1		Shorea robusta
Smilax perfoliata	JF956459.1	JF944425.1	JF978768.1	Smilax sp.
Spondias mombin	AY594480.1	GQ981882.1	AF445882.1	Spondias pinnata
Sterculia apetala	GQ982103.1	JQ594218.1		Sterculia villosa
Stereospermum chelonoides			KF199892.1	Stereospermum chelonoides
Styrax officinalis	AJ429300.1	EU980810.1	AF327489.1	Styrax sp.
Syzygium cumini	GU135062.1		FM887016.1	Syzygium cumini
Syzygium jambos	DQ088583.1	JQ592986.1	AM234135.1	Syzygium jambos
Tectona grandis	FM163282.1	JQ618492.1	FM163255.1	Tectona grandis
Terminalia bellirica		AF425714.1	FJ381773.1	Terminalia bellirica
Terminalia chebula	AB924845.1	FJ381812.1	FJ381775.1	Terminalia chebula
Terminalia myriocarpa		FJ381816.1	FJ381779.1	Terminalia myriocarpa
Tetrameles nudiflora	AY968458.1	AF206828.1	AF280105.1	Tetrameles nudiflora
Toona ciliata	JX518246.1		FJ462488.1	Toona ciliata

Toona sureni			KC155954.1	Toona sureni var. sureni
Toxicodendron griffithii			FJ945925.1	Toxicodendron griffithii
Trema orientalis	JX518199.1	AB925367.1	AY488734.1	Trema orientalis
Trevesia palmata	GQ434261.1	U50258.1	KF591488.1	Trevesia palmata
Trewia nudiflora		AY663648.1	DQ866628.1	Trewia nudiflora
Tsuga dumosa	EF395590.1	AF145460.1	EF395515.1	Tsuga dumosa
Vernonia cinerea		GU724239.1	AY142953.1	Vernonia arborea
Viburnum colebrookeanum	HQ591570.1	HQ591715.1	HQ591959.1	Viburnum colebrookeanum
Viburnum cylindricum	JF956777.1	JF944759.1	JF979002.1	Viburnum cylindricum
Walsura robusta	AB924714.1	AB925325.1		Walsura robusta
Wendlandia tinctoria	HM119580.1	FM207649.1	FM204699.1	Wendlandia glabrata
Zanthoxylum armatum		GQ436751.1	DQ016546.1	Zanthoxylum armatum
Ziziphus mauritiana	JX518013.1	JX856806.1	DQ146589.1	Zizyphus mauritiana

Appendix 3: Example phylogeny.

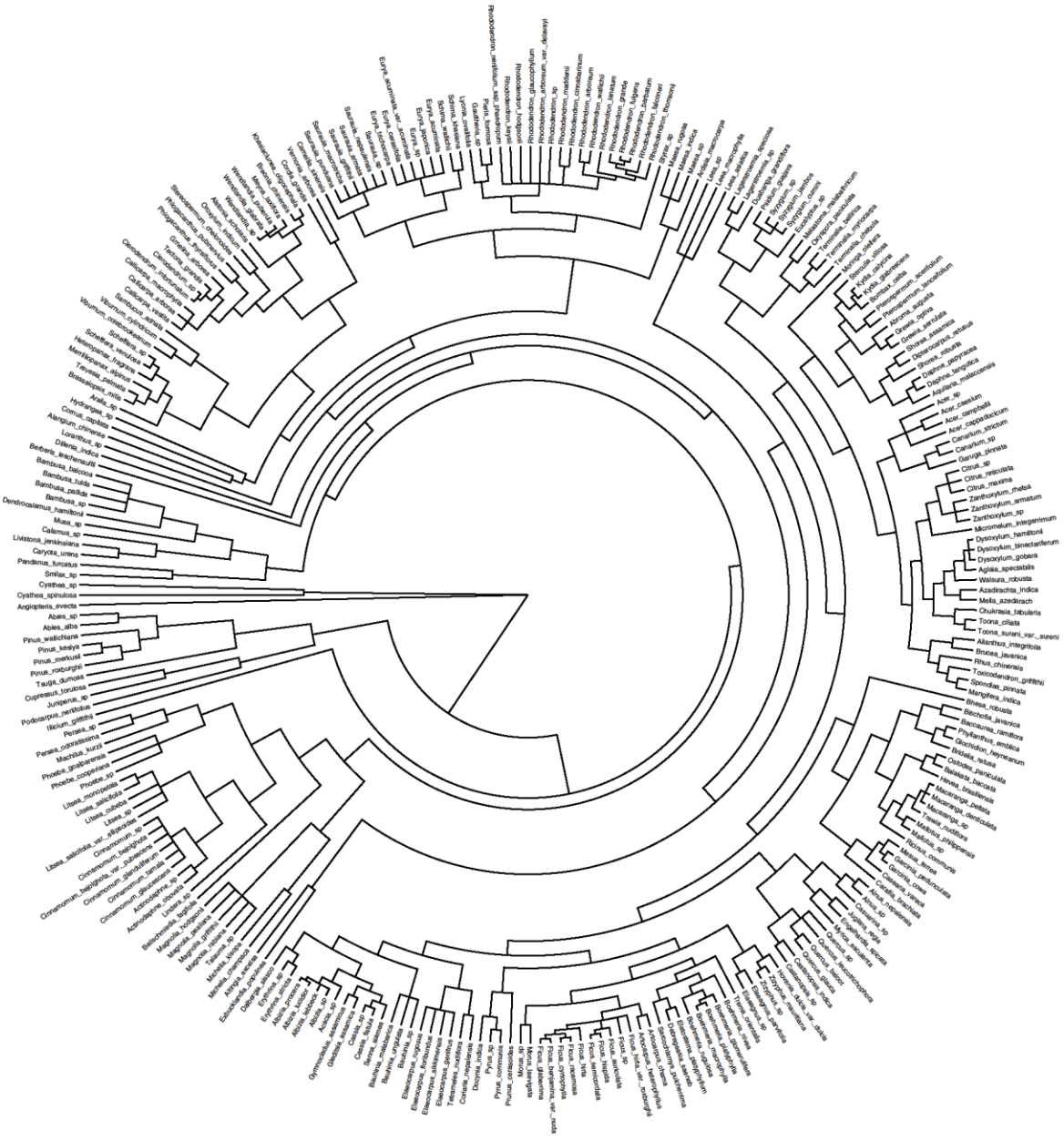

Figure A3: One of the 100 phylogenies used in this study. The phylogenies were built for 279 species and rooted on *Angiopteris evecta*, identified as the most basal species present in our species pool.

Appendix 4: The relationship between the standardized effect size of phylogenetic diversity and elevation.

Glacial refugia may sustain a disproportionate amount of phylogenetic diversity if relict species are phylogenetically unique, perhaps due to the local extinction of closely related species. The standardized effect size of phylogenetic diversity (ses.pd) corrects for species richness and can provide significance with a null model that compares observed phylogenetic diversity to simulated phylogenetic diversity, given species richness and the regional phylogeny. We found that ses.pd increased with log-transformed altitude (R^2_{adj}=0.156, P<0.001). This suggests that plots at high elevations have higher phylogenetic diversity than expected given species richness. Although we find a trend of increasing ses.pd with elevation, the 39/291 plots with significant ses.pd were located throughout the region at elevations ranging from 192m to 3863m. Consequently, there was no relationship between plots with significant PD and elevation (R^2_{adj}=0.002, P=0.299).

Appendix 5: The net-relatedness index with gymnosperms and ferns removed.

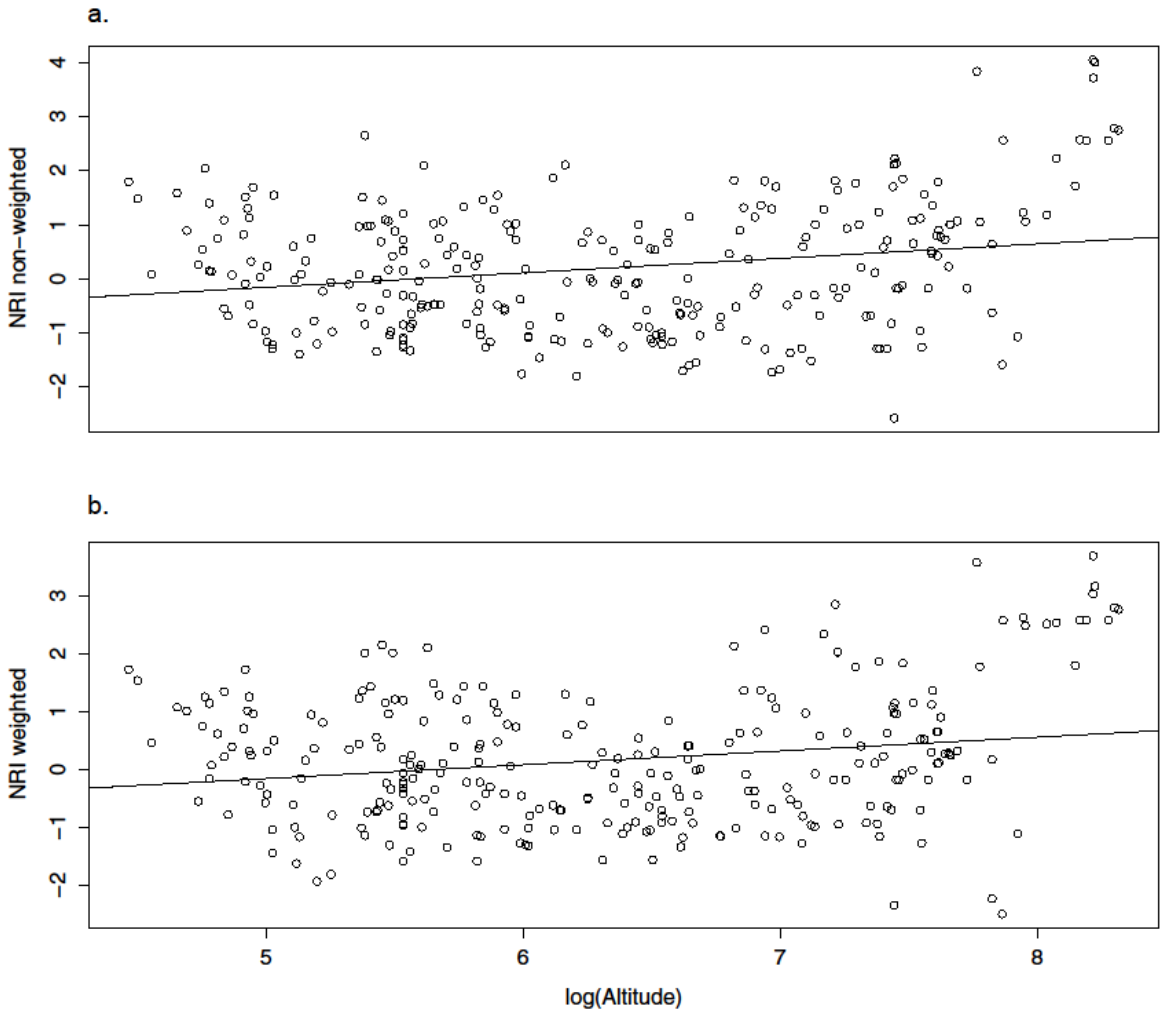

Figure A5: Patterns of net-relatedness index (NRI) along the elevational gradient with gymnosperms and ferns removed from the regional phylogeny and ignored if present in the community plots. Fig. A5a shows the change in non-abundance weighted NRI with log-transformed elevation (linear regression; R^2_{adj}=0.047, P<0.001) while Fig. A5b shows the change in abundance weighted NRI with log-transformed elevation (linear regression; R^2_{adj}=0.038, P<0.001). Although the slope is positive, removing long branch lengths from the analysis did not significantly change our result of no clear pattern of phylogenetic dispersion with elevation. Therefore, it is unlikely that gymnosperms and ferns skewed the patterns of phylogenetic dispersion observed in our study.

Appendix 6: Mantel tests for phylogenetic beta diversity against elevation and distance with gymnosperms and ferns removed.

Table A6: Mantel tests were calculated for pairwise phylogenetic beta diversity (PBD; calculated with *phylosor*) with gymnosperms and ferns removed against elevation, distance or both. Results show strong, negative relationships between phylogenetic beta diversity (shared branch lengths) and elevation, even when correcting for differences in distance, which is consistent with our results when gymnosperms and ferns were included in the analysis.

Model	mantel-r	*P*
PBD~elevation	-0.481	<0.001
PBD~distance	-0.320	<0.001
PBD~elevation + distance	-0.400	<0.001